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## EFFECTS OF TAG LOSS ON DIRECT ESTIMATES OF POPULATION GROWTH RATE

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**Abstract.** The temporal symmetry approach of R. Pradel can be used with capture–recapture data to produce retrospective estimates of a population’s growth rate,  $\lambda_i$ , and the relative contributions to  $\lambda_i$  from different components of the population. Direct estimation of  $\lambda_i$  provides an alternative to using population projection matrices to estimate asymptotic  $\lambda$  and is seeing increased use. However, the robustness of direct estimates of  $\lambda_i$  to violations of several key assumptions has not yet been investigated. Here, we consider tag loss as a possible source of bias for scenarios in which the rate of tag loss is (1) the same for all marked animals in the population and (2) a function of tag age. We computed analytic approximations of the expected values for each of the parameter estimators involved in direct estimation and used those values to calculate bias and precision for each parameter estimator. Estimates of  $\lambda_i$  were robust to homogeneous rates of tag loss. When tag loss rates varied by tag age, bias occurred for some of the sampling situations evaluated, especially those with low capture probability, a high rate of tag loss, or both. For situations with low rates of tag loss and high capture probability, bias was low and often negligible. Estimates of contributions of demographic components to  $\lambda_i$  were not robust to tag loss. Tag loss reduced the precision of all estimates because tag loss results in fewer marked animals remaining available for estimation. Clearly tag loss should be prevented if possible, and should be considered in analyses of  $\lambda_i$ , but tag loss does not necessarily preclude unbiased estimation of  $\lambda_i$ .

**Key words:** *bias; capture probability; capture–recapture; direct estimation of population growth rate; population dynamics; tag loss.*

### INTRODUCTION

The finite rate of population increase or population growth rate,  $\lambda_i$ , and the relative contributions to  $\lambda_i$  from different components of the population can now be estimated directly from open-model capture–recapture data using Pradel’s (1996) temporal symmetry approach and advances presented by Nichols et al. (2000) and Nichols and Hines (2002). Temporal symmetry models simultaneously employ forward-time Cormack–Jolly–Seber (CJS) modeling of survival rate (Cormack 1964, Jolly 1965, Seber 1965) and reverse-time modeling of recruitment (Pollock et al. 1974, Nichols et al. 1986, Pradel 1996) to produce retrospective estimates of  $\lambda_i$ .

As presented by Nichols and Hines (2002), direct estimation of  $\lambda_i$  with the temporal symmetry approach provides an alternative to estimation of asymptotic  $\lambda$

from population projection matrices (e.g., Bernardelli 1941, Lewis 1942, Leslie 1945, Caswell 1989, 2001). Asymptotic  $\lambda$  is often used as a description of the average  $\lambda_i$  during a study. However, there are reasons for being cautious about such use (Nichols and Hines 2002). Accordingly, direct estimation of  $\lambda_i$  is seeing increased use in studies with interest in realized, rather than asymptotic,  $\lambda$  (e.g., Dreitz et al. 2002, Sandercock and Beissinger 2002, Franklin et al. 2004).

Hines and Nichols (2002) reviewed the assumptions of the temporal symmetry approach and investigated the robustness of estimates of  $\lambda_i$  to violations of several key assumptions. Specifically, they reported on the effects of (1) expanding the size of the study area over time; (2) permanent trap response in capture probability; and (3) heterogeneous capture probabilities. However, the effects of tag loss, sampling that is not instantaneous, and temporary emigrations have not yet been investigated. Tag loss has been shown to be a problem in diverse species (e.g., Samuel et al. 1990, Nichols et al. 1992, Diefenbach and Alt 1998, Fabrizio

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et al. 1999). The rate of tag loss may be constant (e.g., Zicus and Pace 1986) or may vary within a group of tagged animals as a function of time since tag application (e.g., Nichols et al. 1992, Diefenbach and Alt 1998, Fabrizio et al. 1999). Given the growing interest in direct estimation of  $\lambda_i$  and contributions of demographic components to  $\lambda_i$  ( $\gamma_i$ , the seniority parameter of Pradel [1996], and functions of  $\gamma_i$ ), and the potential for tag loss in some studies, we conducted this study to evaluate the potential effects of tag loss on direct estimates of  $\lambda_i$  and  $\gamma_i$ . We begin by providing technical background and then evaluate two types of tag loss scenarios: (1) those in which tag loss occurs at a constant rate for all tags at any sampling occasion, and (2) those in which rates of tag loss vary by age of tag.

#### TECHNICAL BACKGROUND

Forward-time models condition on initial captures of animals, whereas reverse-time models condition on the final capture of an individual. For the situation in which there are no losses on capture, the models use the following parameters (see Williams et al. [2002] for additional details). Forward-time models use  $p_i$ , the probability that a marked animal that is alive and in the study population on sampling occasion  $i$  is captured during occasion  $i$ ;  $\phi_i$ , the probability that a marked animal alive in the study population on occasion  $i$  survives until  $i + 1$  and does not permanently emigrate; and  $\chi_i$ , the probability that an animal alive and in the study population during occasion  $i$  is not caught again after occasion  $i$  ( $\chi_K = 1$  for a  $K$ -occasion study; values for occasions  $i < K$  are computed recursively). Reverse-time models use  $p_i$ ;  $\gamma_i$ , the probability that an animal present on sampling occasion  $i$  was present in the study population at time  $i - 1$ ; and  $\xi_i$ , the probability that an animal present at occasion  $i$  is not seen in occasions before  $i$  ( $\xi_1 = 1$ , and  $\xi_i$  for  $i = 2, \dots, K$  are computed recursively). Pradel (1996) termed  $\gamma_i$  the seniority parameter, which is related to recruitment rate,  $f_i$ , as  $\gamma_i = \phi_{i-1}/(\phi_{i-1} + f_{i-1})$ , where  $f_i$  is defined as the number of new animals present at time  $i + 1$  per animal at  $i$ .

Pradel (1996) provided intuition for his estimator of  $\lambda_i$  by equating forward-time and reverse-time model expressions for the expected number of animals present in two consecutive sampling periods,  $i$  and  $i + 1$ . In particular, he noted that this expectation can be written as either  $N_i\phi_i$ , or as  $N_{i+1}\gamma_{i+1}$ , where  $N_i$  is the number of animals in the population at time  $i$ . Equating these expectations and rearranging yields

$$\lambda_i = E\left(\frac{N_{i+1}}{N_i}\right) \approx \frac{\phi_i}{\gamma_{i+1}}.$$

Given these parameters, an alternative expression for  $\lambda_i$  is thus  $\phi_i + f_i$ .

Tag loss is known to negatively bias forward-time estimates of survival unless information on the rate of tag retention is incorporated (Arnason and Mills 1981,

Nichols et al. 1992). Bias associated with tag loss involves the fact that in the modeling of capture history data,  $\phi_i$  is always accompanied by  $\theta_i$ , the probability that an animal alive and wearing a tag at time  $i$  retains its tag until  $i + 1$ , given that the animal survives. Consider the probability associated with the forward-time capture history 101, indicating capture in periods 1 and 3 of a three-occasion study in which tag loss occurs:

$$\Pr\{101 \mid \text{release at occasion 1}\} = \phi_1\theta_1(1 - p_2)\phi_2\theta_2p_3.$$

Every time the animal survives, the tag must survive also in order for us to recapture the animal and know that we have done so. Tag loss also should negatively bias estimates of seniority ( $\gamma_i$ ), and, with respect to reverse-time modeling, it is  $\gamma_{i+1}$  that always must be accompanied by  $\theta_i$ . Consider the probability associated with reverse-time capture history 101, indicating capture in periods 3 and 1 of a three-occasion study with tag loss:

$$\Pr\{101 \mid \text{last caught at occasion 3}\} = \gamma_3\theta_2(1 - p_2)\gamma_2\theta_1p_1.$$

Thus, it is clear that when  $\theta_i < 1.0$ , estimates of  $\phi_i$  and  $\gamma_{i+1}$  will be negatively biased unless adjusted for tag retention rate. Specifically, under the CJS model,  $E(\hat{\phi}_i) = \phi_i\theta_i$  (Arnason and Mills 1981). Similarly, it can be shown that under the time-specific, reverse-time model of Pradel (1996),  $E(\hat{\gamma}_i) = \gamma_i\theta_{i-1}$ .

However, the preceding also indicates that estimates of  $\lambda_i$  may not be biased by tag loss. Note that under the temporal symmetry models of Pradel (1996), e.g., model  $(\phi_i, p_i, \gamma_i)$ ,  $\lambda_i$  can be estimated as a derived parameter,  $\hat{\lambda}_i = \hat{\phi}_i / \hat{\gamma}_{i+1}$ . If we insert the expectations for the survival and seniority parameters in the presence of tag loss, we can approximate the expected value of the derived estimator for  $\lambda_i$  as

$$E(\hat{\lambda}_i) = E\left(\frac{\hat{\phi}_i}{\hat{\gamma}_{i+1}}\right) \approx \frac{\phi_i\theta_i}{\gamma_{i+1}\theta_i} = \frac{\phi_i}{\gamma_{i+1}} = \lambda_i.$$

Thus, if we insert the biased estimates of survival and seniority into the estimator for  $\lambda_i$ , we obtain an approximately unbiased estimate of  $\lambda_i$ . Thus, the effects of tag loss on forward- and reverse-time modeling can be viewed as off-setting when  $\theta_i$ , a single rate of tag loss, affects all tags present in the population between time  $i$  and time  $i + 1$ . However, it is less obvious that the effects of tag loss will be perfectly off-setting if  $\theta_i$  varies among tags, e.g., heterogeneity in  $\theta_i$  related to tag age or tag type. McDonald et al. (2003) showed that tag loss that is related to tag age can bias Jolly-Seber (Jolly 1965, Seber 1965) estimates of population size under some circumstances. Given these results and the fact that Pradel's temporal symmetry approach and the Jolly-Seber approach are simply different parameterizations of the same model, it is possible that estimates of  $\lambda_i$  may be biased by heterogeneous rates of tag loss. Because tag loss will result in there being fewer marked animals under all tag loss scenarios, tag loss is expected to reduce the precision of estimates.

TABLE 1. Approximations for the bias and precision of  $\lambda_i$ ,  $p_i$ ,  $\phi_i$ , and  $\gamma_i$  under model  $(\phi_i, p_i, \gamma_i)$  of Pradel (1996) for cases with no losses on capture, 10 sampling occasions, constant annual rate of tag retention, and time-varying values for  $\lambda_i$ ,  $p_i$ ,  $\phi_i$ , and  $\gamma_i$ .

Parameter	Average bias				Average SE			
	$\theta = 0.75$	$\theta = 0.85$	$\theta = 0.95$	$\theta = 1.00$	$\theta = 0.75$	$\theta = 0.85$	$\theta = 0.95$	$\theta = 1.00$
Capture probability $\bar{p}_i = 0.85$								
$\lambda_i$	0.000	0.000	0.000	0.000	0.073	0.064	0.054	0.050
$p_i$	0.000	0.000	0.000	0.000	0.037	0.033	0.029	0.027
$\phi_i$	-0.187	-0.112	-0.037	0.000	0.034	0.032	0.030	0.028
$\gamma_i$	-0.190	-0.114	-0.038	0.000	0.034	0.032	0.030	0.028
Capture probability $\bar{p}_i = 0.45$								
$\lambda_i$	0.000	0.000	0.000	0.000	0.201	0.169	0.142	0.129
$p_i$	0.000	0.000	0.000	0.000	0.067	0.058	0.051	0.048
$\phi_i$	-0.187	-0.112	-0.037	0.000	0.078	0.074	0.070	0.067
$\gamma_i$	-0.190	-0.114	-0.038	0.000	0.080	0.076	0.071	0.068

Notes: The eight scenarios differed with respect to annual tag retention rate ( $\theta$ ) and average capture probability ( $\bar{p}_i$ ). See *Technical background* for parameter definitions. Parameter values were as follows:  $\lambda_1 = 1.07$ ,  $\lambda_2 = 0.81$ ,  $\lambda_3 = 1.00$ ,  $\lambda_4 = 1.11$ ,  $\lambda_5 = 1.03$ ,  $\lambda_6 = 1.20$ ,  $\lambda_7 = 0.92$ ,  $\lambda_8 = 0.87$ , and  $\lambda_9 = 1.03$ ;  $\phi_1 = 0.75$ ,  $\phi_2 = 0.73$ ,  $\phi_3 = 0.71$ ,  $\phi_4 = 0.78$ ,  $\phi_5 = 0.73$ ,  $\phi_6 = 0.80$ ,  $\phi_7 = 0.75$ ,  $\phi_8 = 0.73$ , and  $\phi_9 = 0.76$ ;  $\gamma_2 = 0.7009$ ,  $\gamma_3 = 0.9012$ ,  $\gamma_4 = 0.7100$ ,  $\gamma_5 = 0.7027$ ,  $\gamma_6 = 0.7087$ ,  $\gamma_7 = 0.6667$ ,  $\gamma_8 = 0.8152$ ,  $\gamma_9 = 0.8391$ , and  $\gamma_{10} = 0.7379$ . For scenarios with  $\bar{p}_i = 0.85$ ,  $p_1 = 0.90$ ,  $p_2 = 0.83$ ,  $p_3 = 0.88$ ,  $p_4 = 0.81$ ,  $p_5 = 0.86$ ,  $p_6 = 0.84$ ,  $p_7 = 0.81$ ,  $p_8 = 0.88$ ,  $p_9 = 0.81$ , and  $p_{10} = 0.90$ . For scenarios with  $\bar{p}_i = 0.45$ ,  $p_1 = 0.50$ ,  $p_2 = 0.43$ ,  $p_3 = 0.48$ ,  $p_4 = 0.41$ ,  $p_5 = 0.46$ ,  $p_6 = 0.44$ ,  $p_7 = 0.41$ ,  $p_8 = 0.48$ ,  $p_9 = 0.41$ , and  $p_{10} = 0.50$ .

## METHODS

We examined the influence of tag loss on  $\lambda_i$  and  $\gamma_i$  using analytic approximations (e.g., Nichols et al. 1981, Burnham et al. 1987, Hines and Nichols 2002) for several representative cases of potential interest, each with 10 sampling occasions. For each scenario examined, we specified parameter values for each sampling occasion and achieved  $N_{i+1}$  (for  $i = 1, 2, \dots, K - 1$ ) by adding the appropriate number of new recruits ( $B_i = N_{i+1} - N_i\phi_i$  where  $N_{i+1} = N_i\lambda_i$ ) to the population at each sampling occasion. No losses on capture occurred and, thus, complications relating to this issue (Williams et al. 2002:469) were not relevant here.

We first evaluated eight scenarios that differed in terms of tag retention rate (four levels) and capture probability (two levels). Annual tag retention rate was constant in each scenario and set at 1.0, 0.95, 0.85, or 0.75 (cases with tag retention rate that varied by year were also investigated but are not reported on here because the results were similar to those for the case of constant  $\theta$ ). All other parameters varied among occasions and ranged as follows:  $\phi_i = 0.71$ – $0.80$  ( $\bar{\phi}_i = 0.75$ ),  $\gamma_i = 0.66$ – $0.90$  ( $\bar{\gamma}_i = 0.75$ ),  $\lambda_i = 0.81$ – $1.20$  ( $\bar{\lambda}_i = 1.00$ ), and  $p_i$  ranged from either 0.40 to 0.50 ( $\bar{p}_i = 0.45$ ) or from 0.80 to 0.90 ( $\bar{p}_i = 0.85$ ) (Table 1). Given an initial population size of 350 animals and the sequence of values for  $\lambda_i$ , expected population size ranged from 303 to 416 over the 10 occasions. The parameter values were used to compute the expected number of animals that would have each observable capture history. Expected numbers were computed using a recursive algorithm coded in C. The algorithm followed a population of animals, exposing them to capture, tag loss once marked, and survival until death or the end of the study, while saving a vector of codes (0, not captured; 1, captured) indicating capture history. The

process was repeated for each cohort of injected animals in capture occasions after the first. The program (GENCAPH1) is available online.<sup>3</sup>

We submitted the expected values for the observable capture histories as fractional numbers to the data-analytic program MARK (White and Burnham 1999) and approximated  $E(\hat{\phi}_i)$ ,  $E(\hat{p}_i)$ ,  $E(\hat{\gamma}_i)$ , and  $E(\hat{\lambda}_i)$  under model  $(\phi_i, p_i, \gamma_i)$ , where  $\hat{\lambda}_i$  was estimated as a derived parameter ( $\hat{\phi}_i/\hat{\gamma}_{i+1}$ ). For the model  $(\phi_i, p_i, \gamma_i)$  and a 10-occasion study, the following parameters can be estimated:  $\phi_1, \phi_2, \dots, \phi_8; p_2, p_3, \dots, p_9; \gamma_3, \gamma_4, \dots, \gamma_{10}$ ; and  $\lambda_2, \lambda_3, \dots, \lambda_8$ . For each scenario, we compared those  $E(\hat{\phi}_i)$ ,  $E(\hat{p}_i)$ ,  $E(\hat{\gamma}_i)$ , and  $E(\hat{\lambda}_i)$  that could be estimated with their respective true parameter values (e.g.,  $\text{Bias}(\hat{\lambda}_i) = E(\hat{\lambda}_i) - \lambda_i$ ) and calculated the maximum and average bias for each parameter across occasions. Because we expected that tag loss would negatively affect the precision of estimates, we also approximated the estimated precision ( $\text{sE}$ ) associated with  $E(\hat{\phi}_i)$ ,  $E(\hat{p}_i)$ ,  $E(\hat{\gamma}_i)$ , and  $E(\hat{\lambda}_i)$  and averaged these for each parameter and scenario.

We investigated the influence of tag loss on  $\lambda_i$  when tag retention rate varied as a function of tag age for two different sets of circumstances. In the first situation, we again used an initial population size of 350 animals and 10 sampling occasions, but held the expected population size constant over all occasions (true  $\lambda_i = 1.0$ , with all  $\phi_i$  and  $\gamma_{i+1} = 0.9$ ) by adding 35 new unmarked animals to the population at each occasion to offset the expected number of deaths, i.e.,  $N_i(1 - \phi_i)$  (see Hines and Nichols 2002). For the first situation, we evaluated nine scenarios that differed in terms of capture probability (three levels: all  $p_i = 0.2, 0.5$ , or  $0.8$ ) and tag retention rates (three levels). Tag retention

<sup>3</sup> (<http://www.mbr-pwrc.usgs.gov/software/gencaph1.html>)

varied by tag age as follows: (1) 0.5, 0.99, 0.98, . . . , 0.92 for tags aged 0, 1, 2, . . . , 9 years, respectively; (2) 0.7, 0.99, 0.98, . . . , 0.92 for tags aged 0, 1, 2, . . . , 9 years, respectively; or (3) 0.9, 0.99, 0.98, . . . , 0.92 for tags aged 0, 1, 2, . . . , 9 years, respectively. This particular pattern of tag loss reflects a high initial loss rate (the type I loss rates of fisheries, e.g., Beverton and Holt 1957) with subsequent loss rates being low but increasing gradually with tag age. Each tagged animal that survived from one occasion to the next, but that lost its tag during the interval, was treated as a new unmarked animal on the next occasion. We submitted the expected values for the observable capture histories as fractional numbers to program MARK (White and Burnham 1999) and approximated  $E(\hat{\lambda}_i)$  and associated estimates of precision under models  $\phi_i$ ,  $p_i$ ,  $\gamma_i$  and  $\lambda_i$ ,  $\phi_i$ ,  $p_i$ , where  $\lambda_i$  indicates that population growth rate was held constant in the model. We compared the  $E(\hat{\lambda}_i)$  that could be estimated with the true parameter value of 1.0 and used these values to calculate the maximum and average bias.

To further evaluate the influence of tag loss on  $\lambda_i$  when tag retention rate varied as a function of tag age, we mimicked the second tag loss model of McDonald et al. (2003) and imposed only immediate tag loss (type I loss) on a population of 500 animals over 10 sampling occasions. Tag retention rate during the year after initial capture was 0.55, 0.75, or 0.95; tag retention rate for tags >1 year old was 1.0. Animals that lost their tags and survived to the next occasion were treated as new animals that were subject to capture and immediate tag loss again. We held the expected population size constant over all occasions (true  $\lambda_i = 1.0$ , with all  $\phi_i$  and  $\gamma_{i+1} = 0.9$  and all  $p_i = 0.2, 0.5$ , or  $0.8$ ) by adding 50 new unmarked animals to the population at each occasion. As in the previous situation, we again used the values of  $E(\hat{\lambda}_i)$  to calculate maximum and average bias for each occasion under each of the nine combinations of tag loss rate (three levels) and capture probability (three levels).

## RESULTS

As predicted, values of  $E(\hat{\lambda}_i)$  were not biased by tag loss that occurred at a homogeneous rate for all tagged animals in the population at a given time. For such scenarios, our estimates of the average and maximum absolute value of bias of  $E(\hat{\lambda}_i)$  from our approximations were < 0.001 for all combinations of  $\theta_i$  and  $p_i$  evaluated (Table 1). Precision of estimates of  $\lambda_i$  was reduced by tag loss, however (Table 1, Fig. 1). As expected, values of  $E(\hat{\gamma}_i)$  were negatively biased by tag loss. Thus, values for the complements of  $E(\hat{\gamma}_i)$  were positively biased, and estimates of the contribution of recruits to population growth were biased high. Although not of primary interest here, as it has been previously shown for forward-time modeling of survival (Arnason and Mills 1981, Nichols et al. 1992), values of  $E(\hat{\phi}_i)$  were also negatively biased by tag loss. In all cases, esti-

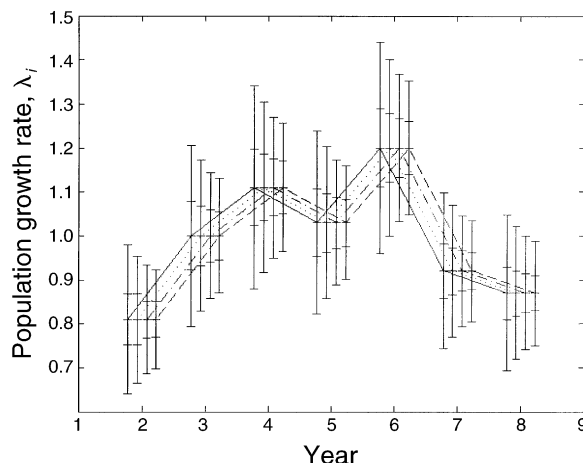


FIG. 1. Approximations of  $E(\hat{\lambda}_i)$  in the presence of tag loss under model  $(\phi_i, p_i, \gamma_i)$  of Pradel (1996) for cases with no losses on capture, 10 sampling occasions, constant annual tag retention rate ( $\theta = 0.75$  [solid line],  $0.85$  [dotted line],  $0.95$  [dot-dashed line], or  $1.0$  [dashed line]), and time-varying values for  $\phi_i$  (range  $0.7$ – $0.8$ ; average  $0.75$ ),  $\gamma_i$  (range  $0.66$ – $0.90$ , average  $0.75$ ),  $\lambda_i$  (range  $0.8$ – $1.2$ , average  $1.0$ ), and  $p_i$  (range  $0.8$ – $0.9$  [average  $0.85$ ]; or range  $= 0.4$ – $0.5$  [average  $0.45$ ]). Initial population size was 350 and subsequent population sizes were dictated by  $\lambda_i$ . Error bars are  $\hat{\lambda}_i \pm 1$  SE, with inner bars for cases with  $\bar{p}_i = 0.85$  and outer bars for cases with  $\bar{p}_i = 0.45$ . See *Technical background* for parameter definitions.

mates of  $\gamma_i$  and  $\phi_i$  could be corrected by dividing  $\hat{\phi}_i$  by  $\theta_i$  and  $\hat{\gamma}_i$  by  $\theta_{i-1}$ . Precision of estimates of  $\phi_i$  and  $\gamma_i$  was reduced by tag loss. Estimates of  $p_i$  were not biased by tag loss that occurred at a homogeneous rate, but associated precision was reduced.

When tag retention rate varied as a function of tag age, approximated values of  $E(\hat{\lambda}_i)$  were biased for some combinations of  $p_i$  and  $\theta_1$ , but were minimally biased or unbiased for others. The bias was greatest for scenarios with low capture probability and high rates of immediate tag loss, and bias was worse early in a study than in later years (Figs. 2 and 3). Because results were similar regardless of whether tag loss occurred with tags of all ages (high immediate loss and low, but gradually increasing, rates of loss for older tags) or only occurred with new tags (immediate tag loss only), we only provide further results for the first circumstance, i.e., where tags of all ages could be lost.

When capture probability was low, bias in  $E(\hat{\lambda}_i)$  could be noteworthy in some but not all cases: e.g., with  $p_i = 0.2$ , bias in  $E(\hat{\lambda}_2)$  ranged from  $-0.060$  (for  $\theta_1 = 0.5$ ) to  $-0.015$  (for  $\theta_1 = 0.9$ ), whereas bias in  $E(\hat{\lambda}_6)$  ranged from  $-0.017$  (for  $\theta_1 = 0.5$ ) to  $-0.001$  (for  $\theta_1 = 0.9$ ). When capture probability was high, bias in  $E(\hat{\lambda}_i)$  was more often minimal although bias was still problematic for early occasions when  $\theta_1$  was low: e.g., with  $p_i = 0.8$ , bias in  $E(\hat{\lambda}_2)$  ranged from  $-0.003$  (for  $\theta_1 = 0.9$ ) to  $-0.033$  (for  $\theta_1 = 0.5$ ), whereas bias in  $E(\hat{\lambda}_6)$  ranged from  $-0.0001$  (for  $\theta_1 = 0.9$ ) to  $-0.001$

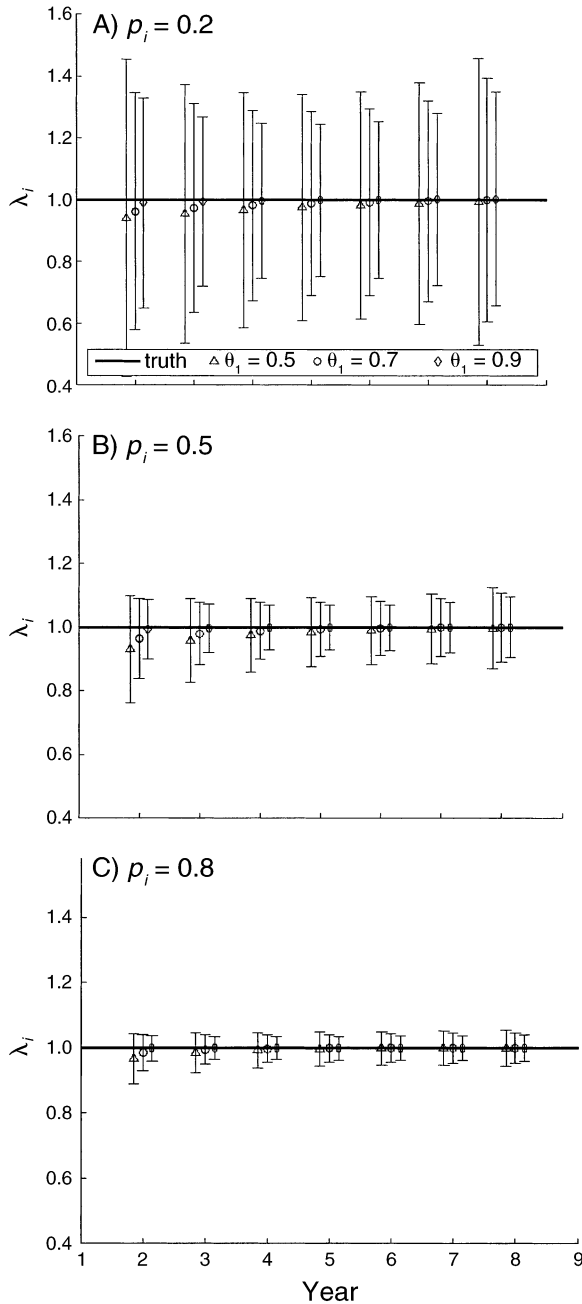


FIG. 2. Approximations of  $E(\hat{\lambda}_i)$  in the presence of tag loss under model  $(\theta_i, p_i, \gamma_i)$  of Pradel (1996) for cases with no losses on capture, 10 sampling occasions, tag loss that was related to tag age (tag retention rate during the year after initial capture  $[\theta_1]$  was 0.5 [triangles], 0.7 [circles], or 0.9 [diamonds]; tag retention rate for tags 1, 2, ..., 8 years old was 0.99, 0.98, ..., 0.92, respectively), and constant values for  $\theta_i$  (0.9),  $\gamma_i$  (0.90),  $\lambda_i$  (1.0), and  $p_i$  (A,  $p_i = 0.2$ ; B,  $p_i = 0.5$ ; C,  $p_i = 0.8$ ). The solid line at 1.0 is the truth. Initial population size was 350, and subsequent population sizes were held constant by adding 35 new individuals to the population at each time step. Error bars are  $\hat{\lambda}_i \pm 1$  SE.

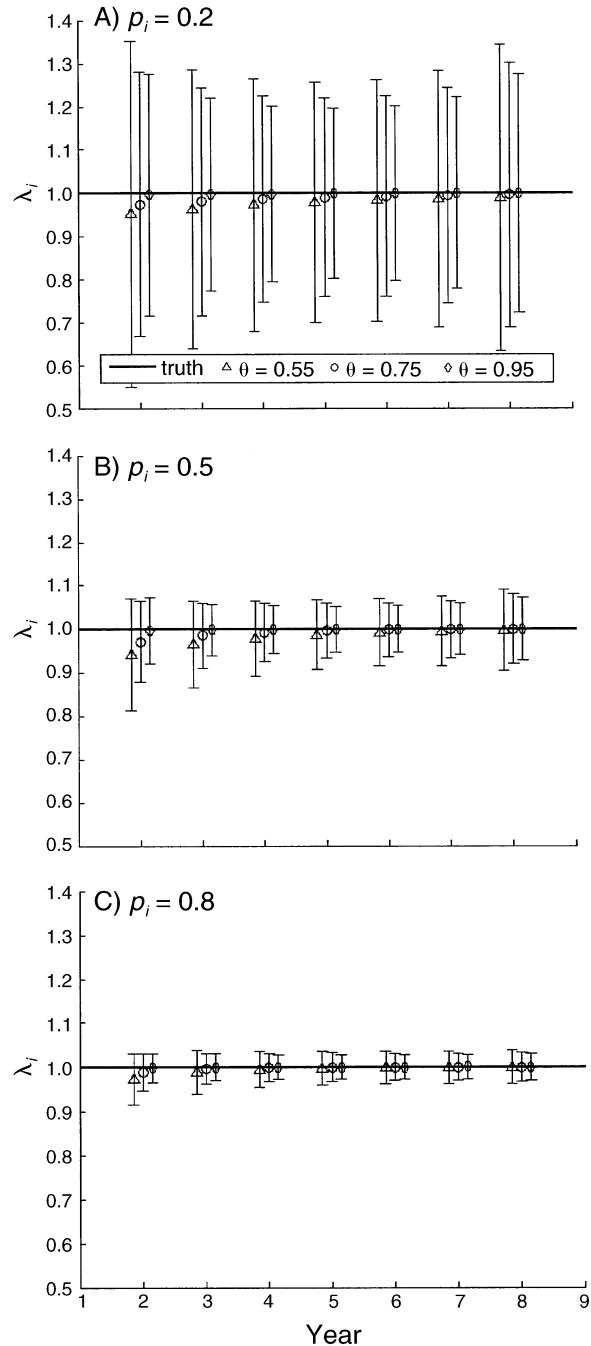


FIG. 3. Approximations of  $E(\hat{\lambda}_i)$  in the presence of tag loss under model  $(\theta_i, p_i, \gamma_i)$  of Pradel (1996) for cases with no losses on capture, 10 sampling occasions, tag loss only in the year immediately following tagging (tag retention rate  $[\theta]$  during the year after initial capture was 0.55 [triangles], 0.75 [circles], or 0.95 [diamonds]; tag retention rate for tags  $>1$  year old was 1.0), and constant values for  $\phi_i$  (0.9),  $\gamma_i$  (0.90),  $\lambda_i$  (1.0), and  $p_i$  (A,  $p_i = 0.2$ ; B,  $p_i = 0.5$ ; C,  $p_i = 0.8$ ). Initial population size was 500, and subsequent population sizes were held constant by adding 50 new individuals to the population at each time step. Error bars are  $\hat{\lambda}_i \pm 1$  SE.

(for  $\theta_1 = 0.5$ ). Estimates of  $E(\hat{\lambda}_i)$  from model  $\lambda_i$ ,  $\phi_i$ ,  $p_i$  provided further evidence of the importance of tag loss rate and capture probability to bias: for  $\theta_1 = 0.9$ , bias in  $E(\hat{\lambda}_i)$  ranged from  $-0.004$  ( $p_i = 0.2$ ) to  $-0.001$  ( $p_i = 0.8$ ), whereas for  $\theta_1 = 0.2$ , bias in  $E(\hat{\lambda}_i)$  ranged from  $-0.026$  ( $p_i = 0.2$ ) to  $-0.006$  ( $p_i = 0.8$ ).

As predicted, the precision of estimates was decreased in the presence of tag loss that was related to tag age (Figs. 2 and 3). For example, in the presence of tag loss that was related to tag age and with  $\theta_1 = 0.5$  and  $p_i = 0.8$ , the average  $s\hat{E}(\hat{\lambda}_i)$  was 0.039 (range 0.037 to 0.043), which was 18% greater than the average  $s\hat{E}(\hat{\lambda}_i)$  of 0.033 (range 0.032 to 0.036) achieved when tag loss did not occur. It is noteworthy that those combinations of  $p_i$  and  $\theta_i$  that led to the most seriously biased  $E(\hat{\lambda}_i)$  also produced imprecise estimates whose associated standard errors were much larger than the associated bias, especially when the full time-varying model ( $\phi_i$ ,  $p_i$ ,  $\gamma_i$ ) was used for estimation. Values of  $E(\hat{\gamma}_i)$ ,  $E(\hat{\phi}_i)$ , and  $E(\hat{p}_i)$  were negatively biased by tag loss that was related to tag age, with the level of bias increasing as tag retention rate and capture probability decreased.

#### DISCUSSION

Four basic conclusions can be drawn from our results. First, estimates of  $\lambda_i$  are robust to homogeneous rates of tag loss. Jolly-Seber estimates of abundance, which can also be used to estimate  $\lambda_i$ , albeit indirectly, also have been shown to be robust to tag loss that is not related to tag age (Arnason and Mills 1981). As noted by Williams et al. (2002), the superpopulation models of Crosbie and Manly (1981) and Schwarz and Arnason (1996) provide an alternative approach for directly estimating  $\lambda_i$ , and the similarity of this approach and that of Pradel (1996) leads one to expect similar results with respect to tag loss and bias.

Secondly, in the presence of heterogeneous rates of tag loss (e.g., rate for a given year varies with tag age), some bias in estimates of  $\lambda_i$  is possible, although the level of bias varies with the rate of tag loss and capture probability. For situations with low rates of tag loss and high capture probability, bias is likely to be low. Bias potentially will be a problem in other scenarios, however. This is similar to what was found by McDonald et al. (2003) with regard to tag loss and Jolly-Seber (Jolly 1965, Seber 1965) estimates of population size. However, we note that estimates of  $\lambda_i$  appear more robust to tag loss than do estimates of population size, which is consistent with the behavior of these estimators under other sources of bias (e.g., heterogeneous capture probabilities; Hines and Nichols 2002). The reasoning underlying this behavior is that estimates of  $\lambda_i$  can be viewed as ratios of abundance estimates,  $\hat{N}_{i+1}$  and  $\hat{N}_i$ . Although the bias in the abundance estimates themselves can be substantial, the relative bias in successive abundance estimates is similar, so these biases

largely cancel to produce relatively robust estimates of  $\lambda_i$ .

Third, tag loss will reduce the precision of estimates of  $\lambda_i$  from the temporal symmetry approach. This is similar to what was found regarding abundance estimates, and thus  $\hat{\lambda}_i$ , based on the Jolly-Seber approach (Arnason and Mills 1981). In studies with high rates of tag loss, low capture probability, or both, the lack of precision on estimates will be a far greater problem than bias. Precision of all parameter estimates is reduced in the presence of tag loss because fewer marked animals remain available for estimation. Thus, it is clearly preferable to design studies such that tag loss does not occur and to evaluate the expected level of bias in  $\lambda_i$  if tag loss is suspected.

Finally, estimates of demographic contributions to  $\lambda_i$  will be biased by tag loss. Thus, researchers will need to incorporate parameters and information about tag loss into capture-recapture models (Nichols et al. 1992, Nichols and Hines 1993) in order to make valid estimates of the relative contributions of different population components based on  $\hat{\gamma}_i$  (Nichols et al. 2000, Nichols and Hines 2002). Clearly, if tag loss is potentially occurring, it is advisable to use double tagging, which will permit estimation of, and adjustment for, tag loss rates, e.g., Nichols et al. (1992).

Given the utility of direct estimates of  $\lambda_i$ , and the relative contributions to  $\lambda_i$  from different components of the population, the use of Pradel's (1996) temporal symmetry approach is likely to increase. Accordingly, further investigations of possible bias resulting from assumption violations would be useful. In particular, it would be valuable to investigate situations concerning non-instantaneous sampling and temporary emigration, as well as other forms of heterogeneity in tag loss rate (e.g., related to animal age).

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